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CLINAL VARIATION IN THE JUVENAL PLUMAGE OF AMERICAN KESTRELS

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Abstract.—The American Kestrel (*Falco sparverius*) is a sexually dichromatic falcon that exhibits considerable individual plumage variability. For example, the anterior extent of the black dorsal barring in juvenile males has been used throughout North America as one of several aging criteria, but recent data demonstrate that the variability among individual Southeastern American Kestrels (*F. S. paulus*) exceeds that accounted for by age. The objective of this study was to search for geographic patterns in the variability of juvenal plumage,

particularly those characteristics considered indicative of age. Nestling kestrels (n = 610) were examined prior to fledging during the 1997 breeding season at nest box programs across a large portion of the North American breeding range. From south to north (1) the crown patches of both males and females become more completely rufous, and (2) shaft streaks on forehead and crown feathers become more pronounced, especially in males. Male Southeastern American Kestrels differed from other males (*F. s. sparverius*) in that the anterior extent of dorsal barring averaged less but was more variable. The variability observed in North America appears to be part of a cline extending across the species range in the Western Hemisphere, where tropical subspecies are small and have reduced dorsal barring. Both body size and, especially in males, dorsal barring increases with increasing north and south latitude. We suggest that this geographic pattern is adaptive in terms of thermoregulation, and that differences in the sex roles may explain why males become less barred with maturity while females do not.

VARIACIÓN CLINAL EN EL PLUMAJE DE LOS JUVENILES DE *FALCO SPARVERIUS*

Sinopsis.—El falcón americano (*Falco sparverius*) es una especie dicromática que exhibe un variacion individual considerable. En los juveniles, por ejemplo, la parte anterior de las barras negras dorsales ha sido utilizada a través de toda Norte América como uno de los criterios para determinar la edad de éstas aves. Sin embargo, datos recientes han demostrado que la variabilidad entre individuos del sureste (*F. s. paulus*), excede los parámetros para determinar la edad. El objetivo de este trabajo fue determinar si había patrones geográficos en la variabilidad del plumaje juvenil, en particular aquellas caracteristicas consideradas indicadores de la edad. Durante el 1997, y virtualmente a todo lo largo de Norte América, se examinaron 610 pichones (previo a que estos dejaran el nido). Se encontró que de sur a norte el parche de la corona en ambos sexos se torma bermejo de forma más completa, y en segundo lugar las rayas de las plumas de la frente y la corona se tornan más pronunciadas, particularmente en los machos. La subespecie del sureste de los E.U.A. se diferencia de los machos de *F. s. sparverius* en que la extención de las barras dorsales anteriores promedió menos pero fue más variable. La variabilidad observada en Norte América parece ser parte de un clin que se extiende a lo largo de la distribución de la especie en el hemisferio occidental, en donde las subespecies tropicales son pequeñas y tienen patrones, en sus barras dorsales más reducidos. Tanto el tamaño corporal como las barras dorsales, particularmente en los machos, aumenta según incrementa la latitud tanto al norte como al sur. Es posible que este patrón geográfico sea adaptativo en términos de termoregulación. La diferencia en el rol de los sexos podría explicar la razón por la cual se reduzcan las barras en los machos, y no en las hembras, según éstos maduran.

The American Kestrel (*Falco sparverius*) is the smallest and most common falcon in North America, and it is the only kestrel species native to the Western Hemisphere, where as many as 17 subspecies are recognized (Bird and Palmer 1988, White et al. 1994). Kestrels are sexually dichromatic, presumably as the result of sexual selection, and they exhibit a large degree of individual plumage variability. Several plumage characteristics are age-related, including the extent of the black dorsal barring and the pattern of ventral streaking in males, and the width of the subterminal black band on female rectrices. These characteristics were incorporated into keys for age and sex determination (U.S. Fish and Wildlife Service 1980, Smallwood 1989). Other characteristics suggested to be indicative of age include the color of the terminal band on male rectrices, the amount of rufous feathering on the crown, and the occurrence of dark shaft streaks on crown feathers (Bent 1938, Parkes 1955, Grossman and Hamlet 1964, Brown and Amadon 1968, Clark and Wheeler 1987).

Kestrels are secondary cavity nesters and readily accept wooden nest

TABLE 1. Study areas and number of nestling American Kestrels examined.

Region	Study area	*n*	Principal investigators[a]
Northern plains	central Saskatchewan	47	GRB
Inter-mountain	southwestern Idaho	184	KS
	northcentral Utah	68	CDM
Central	central Iowa	67	MM
Mid-Atlantic	eastern Pennsylvania	81	RR, SR
	northwestern New Jersey	78	JAS, CN
Southeast	southeastern Georgia	20	WRS, SAL
	northcentral Florida (Suwannee, Levy counties)	52	RJM
	northcentral Florida (Clay County)	13	BT

[a] GRB = G. R. Bortolotti, KS = K. Steenhof, CDM = C. D. Marti, MM = M. Meetz, RR = R. Robertson, SR = S. Robertson, JAS = J. A. Smallwood, CN = C. Natale, WRS = W. R. Shuford, SAL = S. A. Lindemann, RJM = R. J. Melvin, and BT = B. Tornwall.

boxes for breeding. Recently, Miller and Smallwood (1997a) reported that approximately half of the nestling male Southeastern American Kestrels (*F. s. paulus*) they examined from nest boxes in northcentral Florida lacked the barring on the anterior half of the dorsum characteristic of juvenal plumage for kestrels from other regions of the continental United States and Canada (*F. s. sparverius*). Therefore, the objective of this study was to search for geographic patterns in the variability of juvenal plumage, particularly those characteristics considered indicative of age.

METHODS

Study areas.—The present study used data from kestrel nest box programs located in nine study areas in the United States and Canada (Table 1). Descriptions of the study areas have been published previously: Saskatchewan (Bortolotti 1994), Idaho (Steenhof and Peterson 1997), Utah (Marti 1997), Iowa (Varland et al. 1991), Pennsylvania (Klucsarits et al. 1997), New Jersey (Smallwood and Wargo 1997), Georgia (Breen and Parrish 1997), and Florida (Miller and Smallwood 1997b).

Plumage characteristics.—We examined nestling kestrels between 12 May 1997 and 10 Sep. 1997, generally when they were 20–25 days of age. We quantified four plumage characteristics, based on visual evaluations. The completeness of the rufous crown patch for males and females was scored from 0–4: 0 = an entirely blue-gray crown, without any rufous feathers; 1 = a blue-gray crown with a few rufous feathers; 2 = an approximately equal number of blue-gray and rufous feathers; 3 = a distinct rufous patch invaded by only a few blue-gray feathers; and 4 = a distinct rufous patch not invaded by any blue-gray feathers. The amount of crown and forehead feather shaft streaks for males and females was scored 0–4: 0 = no shaft streaks, 1 = a few feathers with shaft streaks, 2 = approximately half of the feathers with shaft streaks, 3 = most feathers with shaft streaks,

and 4 = all feathers with shaft streaks. In males we measured how far anteriorly the black bars extended from the rump or upper tail coverts toward the nape: 0% = no dorsal barring, 25% = barring limited to posterior quarter of dorsum, 50% = posterior half of dorsum barred, 75% = posterior three quarters of dorsum barred, 100% = dorsum barred anteriorly to the nape. In females, the width of the subterminal black band on rectrices, excluding the central and outer pairs, was compared to the width of the immediately basal black band, and was measured in increments of 0.25 (Smallwood 1989).

Data analysis.—Data from the nine study areas were pooled into five regions (Table 1) for analysis. Because significant deviations from normality were detected, we employed nonparametric treatments. For each variable, we tested for differences among regions with Kruskal-Wallis tests, and subsequently conducted all pair-wise comparisons of regions with Wilcoxon rank sum tests. Statistical significance was set at $P < 0.05$, and P-values for pair-wise comparisons were adjusted to control for the experimentwise error rate using Bonferroni's probabilities (Snedecor and Cochran 1980).

Each of the nine study areas had different individuals, or groups of individuals, visually evaluating plumage characteristics. Thus, there was the possibility that differences among study areas could be confounded with observer bias. This possibility was reduced by pooling the study areas into five regions for analysis, so that the statistical treatments (regions) would include data collected by multiple observers. However, two regions (northern plains and central) each were represented by single study areas. To further address the possibility of observer bias, we calculated the mean intra-regional differences between study areas for each variable in the three regions consisting of multiple study areas. This intra-regional variability provides a measure by which inter-regional differences may be compared.

RESULTS

We examined a total of 610 nestling kestrels (294 males, 316 females). Scores for completeness of the rufous crown patch ranged from 0–4 in both males and females. Northern plains males had the most complete rufous patches (mean score = 3.63 ± 0.60 SD), and crown patch scores decreased significantly toward the east and southeast regions (Fig. 1). Half of all southeastern males had scores of 0 or 1 (mean score = 1.68 ± 1.07 SD). We detected a similar trend in females; crown patch scores were greatest in the northern plains (mean score = 3.25 ± 1.14 SD), and the northern plains and inter-mountain regions had significantly greater scores than the three central and eastern regions.

Scores for the amount of crown streaking in females ranged from 0–4 in every region, and the differences among regions were significant (Fig. 2), with the most pronounced streaking in the northern plains (mean score = 3.43 ± 1.29 SD). Crown streaking scores for the northern plains and inter-mountain regions were significantly greater than those of the

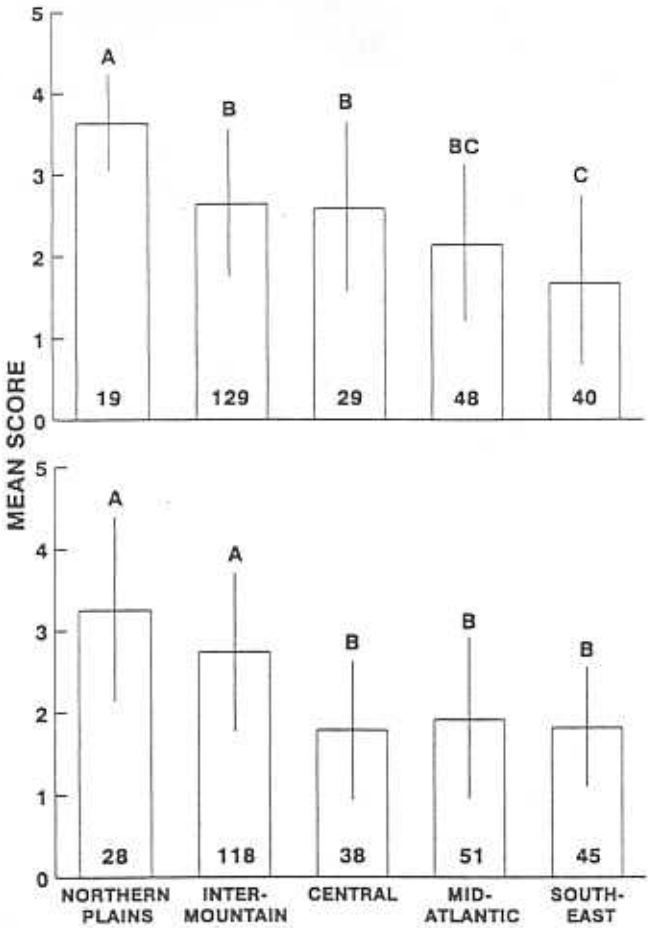

FIGURE 1. Rufous crown patch scores for male (top) and female (bottom) juvenile American Kestrels. 0 = blue-gray crown, 4 = rufous crown (see text for complete definitions). Vertical lines are ±1 SD. Numbers indicate sample size. Bars with same letter are not significantly different (10 pair-wise Wilcoxon rank sum tests, $P > 0.05$, adjusted for Bonferroni's inequalities).

three central and eastern regions, and no significant difference was detected between the central (mean score = 1.61 ± 1.13 SD) and southeastern regions (mean score = 1.87 ± 1.32 SD). Scores for the amount of crown streaking in males also ranged from 0–4 in each region except the northern plains, where the minimum score was 1 (mean score = 2.89 ± 0.81 SD), and the southeast, where the maximum score was 2 (mean score = 0.63 ± 0.59 SD); the differences among regions also were significant.

The dorsal barring in males exhibited a significant north to south trend (Fig. 3). All northern plains males examined had barring that extended entirely (100%) from rump to nape. Southeastern males had the least extensive barring (mean percent = 60.6%) and were the most variable

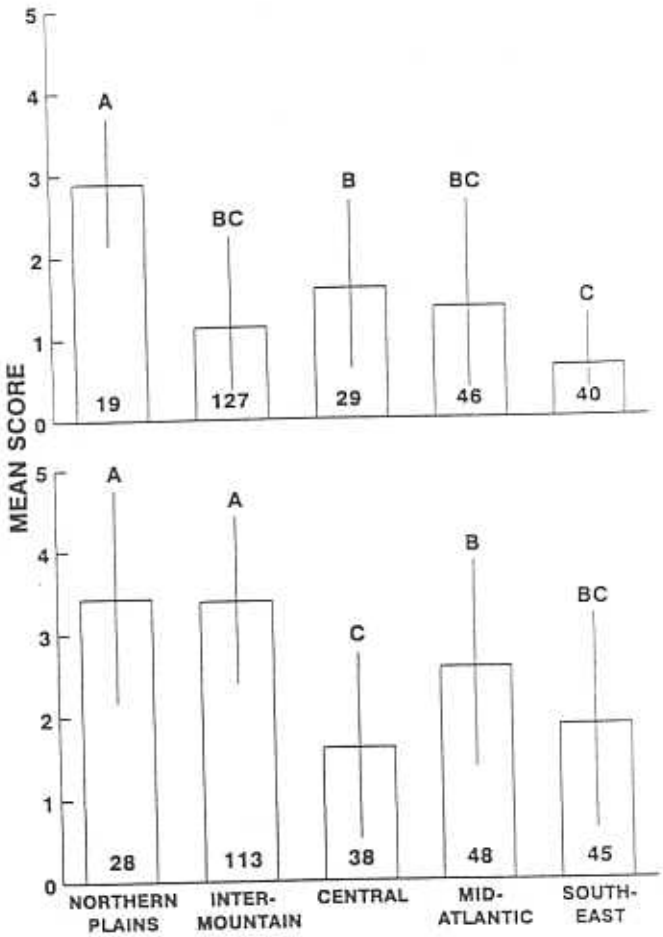

FIGURE 2. Crown streaking scores for male (top) and female (bottom) juvenile American Kestrels. 0 = no dark shaft streaks on crown feathers, 4 = dark shaft streaks on all crown feathers (see text for complete definitions). Vertical lines are ±1 SD. Numbers indicate sample size. Bars with same letter are not significantly different (10 pair-wise Wilcoxon rank sum tests, $P > 0.05$, adjusted for Bonferroni's inequalities).

(SD = 32.5) in this regard. Males from the three mid-latitude regions were intermediate, differing significantly from males both to the north and to the south. Males with barring restricted to the posterior half of the rump to nape distance represented 7.7%, 3.4%, 9.7%, and 42.5% of the samples from the inter-mountain, central, mid-Atlantic, and south-eastern regions, respectively.

We detected significant differences among regions in the relative width of the subterminal black band in female rectrices (Fig. 4). The widest bands were observed in the inter-mountain region (mean width = 1.79 ± 0.68 SD), and the narrowest in the northern plains (mean width = 1.37 ± 0.48 SD) and southeast regions (mean width = 1.30 ± 0.48 SD).

The mean intra-regional variability (mean differences between study

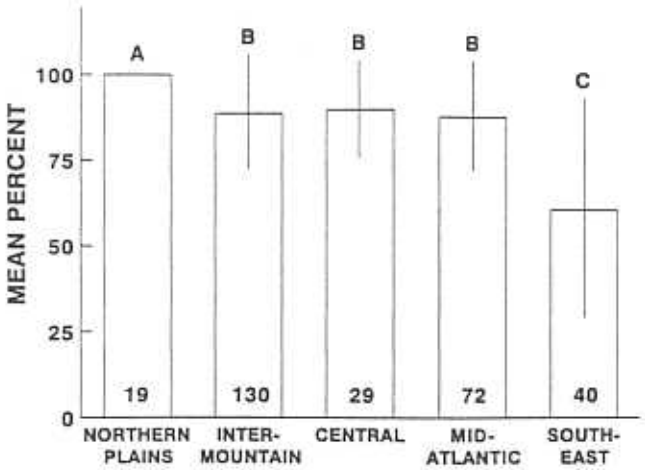

FIGURE 3. Extent of dorsal barring for juvenile male American Kestrels. 0% = no black barring on dorsum, 100% = entire region from rump to nape barred. Vertical lines are ±1 SD. Numbers indicate sample size. Bars with same letter are not significantly different (10 pair-wise Wilcoxon rank sum tests, $P > 0.05$, adjusted for Bonferroni's inequalities).

areas) for rufous crown patches in males, rufous crown patches in females, crown streaking in males, crown streaking in females, dorsal barring in males, and subterminal black band width in females was 0.884, 0.635, 0.551, 1.392, 0.098, and 0.470, respectively. All significant pair-wise differences ($n = 35$) between regions exceeded the corresponding intra-regional variability, with the exception of crown streaking in females (mid-Atlantic versus northern plains, inter-mountain, and central regions) and

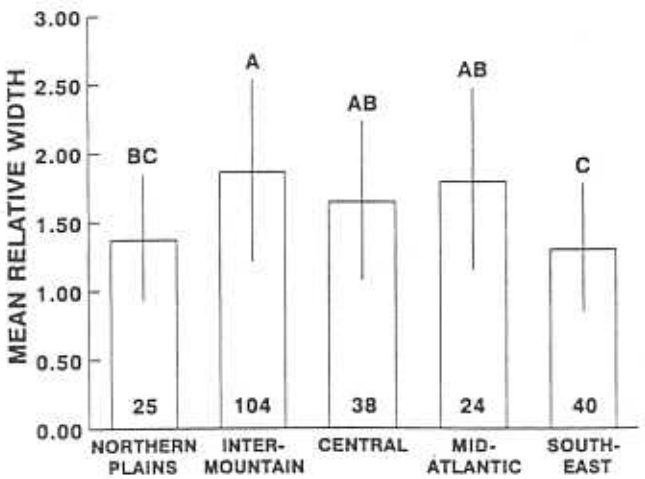

FIGURE 4. Width of black subterminal black on second through fifth pairs of rectrices for juvenile female American Kestrels. Width is relative to next (basal) black band. Vertical lines are ±1 SD. Numbers indicate sample size. Bars with same letter are not significantly different (10 pair-wise Wilcoxon rank sum tests, $P > 0.05$, adjusted for Bonferroni's inequalities).

subterminal black band width in females (central versus southeast regions).

DISCUSSION

The calculated differences in plumage characteristics between study areas within a region are the sum of actual differences and any observer bias that may exist. True variability is expected between the study sites, which were separated by as much as 400 km (i.e., the Idaho and Utah sites). Because migratory populations of *F. s. sparverius* tend to be philopatric (Bowman et al. 1987), gene flow is expected to be greater within a study area than between areas. Further, kestrels in the southeastern region, *F. s. paulus*, presumably are nonmigratory (Smallwood 1990) and exhibit both short-distance natal dispersals and a high degree of site fidelity (Miller and Smallwood 1997b). The study areas in Florida and Georgia were separated by approximately 300 km, which likely restricts gene flow between these populations. Thus, using mean intra-regional variability as the standard by which inter-regional differences may be compared is a conservative method of addressing possible observer bias.

Because most of the inter-regional differences in crown and dorsal plumage characteristics were large (relative to intra-regional variability), and because these characters varied regularly with latitude and longitude, the observed variability in kestrel juvenal body plumage may be considered, in part, a cline. The amount of rufous in the crown decreased from northwest to southeast in both sexes, although more uniformly so in males. This pattern is consistent with the north-south trends among other kestrel subspecies. Compared to *F. s. sparverius*, the rufous crown feathering tends to be reduced or absent in the populations of Caribbean Islands (e.g., *F. s. sparvoides, F. s. dominicensis*; Grossman and Hamlet 1964), southern Mexico, Guatemala, northern Honduras (*F. s. tropicalis*, Brown and Amadon 1968), and northeastern Nicaragua (*F. s. nicaraguensis*, Cade 1982). Similarly, the amount of streaking in the crown feathers tended to be greatest in the north and west.

There was a significant and uniform latitudinal trend in the dorsal barring of males. Although the degree to which extensive black barring increases heat absorption through insolation is unknown, the pattern we observed is in the direction predicted by thermal considerations. Moreover, the geographic pattern we observed in our study areas in North America appears to be a continuation of the trend seen in more southern kestrel subspecies. Kestrels that breed in the desert region of the southwestern United States (formerly *F. s. phalaena*) are paler than the more northern *F. s. sparverius*, and kestrels from Baja California, Sonora, and Sinaloa, Mexico (*F. s. peninsularis*) are paler still, and with even less barring (Bent 1938). The same trend in barring and overall color is evident in the east, from *F. s. dominicensis* of Hispaniola to *F. s. isabellinus* of eastern Venezuela and northern Brazil (Brown and Amadon 1968).

Because of differences in breeding roles, male kestrels may benefit more than females by a reduction of dorsal black pigmentation in lower

latitudes where sunlight is more direct. Males typically provide a substantial amount of food to their mates prior to egg laying and during incubation (Balgooyen 1976). In contrast, females perform most of the incubation, brooding, and caring for small young; as cavity nesters, they perform these activities in shade. Thus, during the breeding season males are constrained to spend considerably more time hunting (Balgooyen 1976), typically from exposed perches. Notably, in the lowland pine savannah of northeastern Nicaragua, female kestrels also have reduced dorsal barring (Cade 1982). The differences in sex roles may also explain why dorsal barring decreases with maturity in males, but not in females.

The trend in dorsal barring closely follows a trend in body size, presumably also an adaptation to the thermal environment. Body size decreases from Canada through Mexico and the Caribbean, is minimal in tropical lowlands, and then increases with increasing latitude and altitude in the Southern Hemisphere (Brown and Amadon 1968, Cade 1982). *F. s. cinnamominus*, which breeds in southern South America to Tierra del Fuego, is not only larger, but also has more dorsal barring than that of subspecies from northern South America (Brown and Amadon 1968).

The specific combinations of alleles that determine an individual kestrel's plumage pattern is unknown. Thus, it may be that rufous coloring and streaking in crown feathers are linked to each other or to dorsal barring, and that the more extensive streaking in birds from higher latitudes may be a manifestation of overall darker dorsal pigmentation. Similarly, the reduced dorsal barring we observed in nestling males in the southeast may be linked to the reduced barring characteristic of the basic plumage acquired later.

The extent of dorsal barring in males, in conjunction with other plumage characteristics, is used as an aging criterion in age-sex keys for North American kestrels (U.S. Fish and Wildlife Service 1980, Smallwood 1989); an unbarred upper one-third to one-half of the back and inter-scapular region is considered indicative of basic plumage. Thus, if dorsal barring were used as the only aging criterion for males (which is not recommended), all of the juveniles in the northern plains sample would be correctly identified while 3.4–9.7% of the mid-latitude males and nearly half (42.5%) of the southeastern males would be incorrectly identified as adults.

Significant differences in the relative width of the black subterminal band of female rectrices were detected among regions, but no consistent geographic pattern was apparent. It is unlikely that the width of this band is related to the thermal environment, nor is another adaptive function evident.

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